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Alternative functional strategies and altered carbon pathways facilitate broad depth ranges in coral-obligate reef fishes

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Abstract:

1. Spatial refuges in peripheral habitats will become increasingly important for species persistence as climate change and other disturbances increasingly impact habitat quality and assembalge compositions. However, the capacity for persistence will be determined in part by species-specific abilities to absorb costs related to altered or decreased quantities and quality of resources at range peripheries.

2. We compare variations in dietary strategies and energy acquisition tradeoffs along depth gradients in two obligate corallivores that differ in level of diet specialization. We also assess depth-related changes in energy pathways and energy content of their mixotrophic prey. We found no changes in feeding effort or total resource availability (total coral cover) toward deep range margins, but availability of the preferred resource (*Acropora* coral) decreased. While both species selectively targeted *Acropora*, the more specialized species (*Chaetodon baronessa)* exhibited limited feeding plasticity along the depth gradient. The degree of selectivity toward the preferred coral increased rather than decreased with depth, being 40 times greater than expected, given availability, at their range periphery. In contrast, the generalist's diet (*C. octofasciatus*) varied greatly in response to changes in resource availability with depth.
3. Unexpectedly, the energy content of *Acropora* did not decline with depth, likely due to increased coral heterotrophy in deeper water, indicated by shifts in their molecular isotope geochemistry. This shift was accompanied by a 20 % increase in plankton-sourced carbon in the muscle tissue of deep-resident fish, despite no observations of direct feeding on plankton food sources.
4. Our results indicate that deep ranges in coral-obligate reef fishes are supported by multiple mechanisms of trophic versatility in both the fish and corals. This nutritional plasticity likely serves a compensatory role in the resilience and eventual adaptation of organisms at their range peripheries.
5. For species vulnerable to increasing anthropogenic impacts at range cores, variable and multi-trophic functional responses can act to buffer against costs and increase the refuge potential of range peripheries. Specialist consumers may

also be supported indirectly at range margins via trophic plasticity within their preferred prey.

Introduction:

Asymmetric habitat declines and range shifts related to rapid environmental change will result in an increasingly larger proportion of species' populations living at current range margins (Thomas et al. 2004, Harris and Pimm 2008, Angert et al. 2011). As environments change, species with viable populations at range margins may demonstrate greater resilience and long-term persistence (i.e. a refuge effect) (Keppel et al. 2012, Reside et al. 2014). However, range peripheries are commonly associated with natural reductions in the quantity and quality of resources (Brown 1984, Thomas and Kunin 1999) that often result in costs to consumers (Zammuto and Millar 1985, Badyaev and Ghalambor 2001). Consequently, understanding potential tradeoffs and compensatory mechanisms of energy acquisition at range peripheries will be vital for predicting future trajectories of species vulnerable to extirpation and extinction.

For energy maximizing species (Hixon 1982), the ability to persist in marginal habitats is likely to rely on flexibility in diets or feeding rates (Flesch and Steidl 2010, Goldstein et al. 2017). Shifts in resource availability in response to disturbances and environmental gradients tend to result in shifts in consumer communities that favor resource generalists over specialists (Clavel et al. 2011). For example, forest cover reductions in the Brazilian Atlantic Forest resuls in greater losses of more specialized insectivorous and fruigivorous birds than habitat and diet generalists (Morante-Filho et al. 2015). Similarly, high elevation habitats that often constitute range margins are dominated by dietary generalists among wood-boring beetles, pollinator bees, and

74 butterflies (Pellissier et al. 2012, Rasmann et al. 2014). Comparisons of dietary
75 strategies and tradeoffs at range peripheries among species with differential
76 specialization can therefore provide insight into the ecological mechanisms that drive
77 broad distributions and refuge potential at range margins.
78
79 Natural environmental gradients provide ideal systems for testing hypotheses regarding
80 the functional response of species to environmental variation (Keppel et al. 2012,
81 Goldstein et al. 2016). Reduced energy acquisition at range margins can occur due to
82 declines in either the availability or quality (e.g. decreased nutrients or energy
83 availability) of preferred resources (Thomas and Kunin 1999). Generalists often exhibit
84 flexible phenotypic responses to prevailing environmental conditions or declining
85 resources in suboptimal and variable conditions, conferring advantages over inflexible
86 specialists (Sol et al. 2002). Therefore, where distribution, resource availability, and
87 disturbance gradients intersect, specialists are theoretically more vulnerable to decline
88 due to the dual pressures of habitat disturbance at the range core and resource limitation
89 at the range periphery (Williams et al. 2008, Moritz and Agudo 2013).
90
91 Functional strategies are not always consistent across environmental gradients (Chevin
92 and Lande 2011, Goldstein et al. 2017). Even species exhibiting high specialization at
93 the range core may demonstrate greater flexibility at the range periphery. Decreased
94 dietary specialization at range margins may facilitate greater resistance to population
95 decline than predicted from observations at the range core (Kawecki 2008). However,
96 investigations of compensatory dietary strategies at range peripheries are rare,
97 particularly among specialized taxa considered vulnerable to habitat degradation and
98 loss of preferred food sources.

Coral reefs are subject to steep declines in light energy and photosynthetic productivity that result in rapid turnover of coral assemblages over small vertical spatial scales (tens of meters). Major faunal breaks in depths of 30-60 m associated with altered metabolic pathways are likely to result in declines in both the quantity and quality of resources available to coral consumers (Anthony et al. 2002, Hoogenboom et al. 2010). Moreover, although coral reefs are increasingly affected by anthropogenic climate change (Bellwood et al. 2004, Hughes et al. 2018), many stressors such as warm-water coral bleaching and storm damage attenuate with depth (Bak et al. 2005, Muir et al. 2017, Baird et al. 2018). Butterflyfishes, the most speciose family of coral consuming reef fishes, offer an ideal model group to assess dietary variation and plasticity responses to environmental and resource gradients among contrasting functional strategies (Nowicki et al. 2013). Butterflyfishes occupy a broad spectrum of dietary specialization on corals, and their conspicuous feeding bouts enable observations of relative feeding effort on different resources (Pratchett 2013). Coral-feeding specialists are vulnerable to population declines following coral loss in shallow water, due to a lack of capacity to shift to alternate resources (Pratchett et al. 2006, Wilson et al. 2006), and their population abundance iappears to be more skewed toward shallow water than coral-feeding generalists (MacDonald et al. 2016, 2018a) (Supplemental figure S1). The combination of low population abundance and decreased availability of their preferred coral prey suggests deep reefs are unlikely refuges for specialized corallivorous butterflyfishes. However, recent studies show that even the most specialized species can occur over broad depth ranges (e.g. 0-40 m) (MacDonald et al. 2016, Suplemental figure S1). Consequently, dietary flexibility along a depth gradient may facilitate the persistence of refuge populations in deeper water following disturbance, thereby

mediating local extinction risks. Depth-related dietary flexibility has been demonstrated for non-coral associated generalist planktivorous (Goldstein et al. 2017) and invertivorous (Bradley et al. 2016) reef fishes. However, the extent to which dietary flexibility across depth may mediate population declines in highly vulnerable coral-obligate species remains unknown.

Here, we examine whether flexibility in diets and/or feeding rates along a depth gradient could facilitate broad depth distributions in obligate corallivores, and therefore be a mechanism in mediating vulnerability to disturbance-induced population collapse. We focus on two butterflyfish species with wide depth ranges but divergent ecological niches and dietary breadths. Specifically we investigate whether: 1) total resource quantity and feeding effort vary with depth; 2) changing resource composition along the depth gradient results in dietary flexibility; 3) changes in resource availability result in reduced feeding effort on, or selectivity for, preferred resources; and 4) corals in deeper water exhibit compensatory mechanisms of energy provision that may be transferred to coral consumers at the deep range periphery.

Methods:

Study site and species

The study was done in Kimbe Bay, Papua New Guinea between May and December, 2015. The vertically continuous coral habitats along the entire depth gradient of Kimbe Bay reefs present no physical barriers to species distributions, therefore depth distributions of species are unlikely to be influenced by dispersal limitation. All observations and samples were collected along the entire depth-gradient on all reefs.

149 We examined two butterflyfish species, *C. baronessa* and *C. octofasciatus*. Both are
150 obligate coral-feeders but have differing levels of dietary specialization (Pratchett 2013,
151 Madduppa et al. 2014). While both species occur across a broad depth range (>30 m),
152 territories of paired individuals span relatively narrow depth ranges (both species ~7 ±
153 0.5 m (mean ± SE), MacDonald et al. 2018). Both species also show contrasting
154 abundance along the depth gradient within their range (Suplemental figure S1): *C.*
155 *baronessa* is most abundant in shallow water (< 5 m) and declines with increasing
156 depth, while *C. octofasciatus* is least abundant in water < 5m and 40m, and most
157 abundant at 20m. The feeding ecology of the two species in shallow waters also
158 contrasts: *C. baronessa* is a dietary specialist that strongly selects corals of the genus
159 *Acropora* (Pratchett 2013), while *C. octofasciatus* feeds on a much broader range of
160 coral taxa (Ghaffar et al. 2006), but does show some preference for *Acropora*
161 (Madduppa et al. 2014). Together, these patterns enable examination of variation in
162 dietary and feeding ecology among depths.
163
164 *Data collection*
165
166 *Depth patterns in resource quantity and composition*
167 To examine broad-scale spatial patterns in potential coral prey across Kimbe Bay, we
168 quantified the abundance (as % cover) of all hard corals and of the preferred dietary
169 genus *Acropora* from 1m^2 photo-quadrats at 5 depths (<1 m, 5 m, 10 m, 20 m, and 30
170 m) on 10 reefs across Kimbe Bay (Suplemental figure S2; see MacDonald et al. (2016)
171 for complete methods). To assess variation in resource composition along the depth
172 gradient, we recorded the availability of 9 key coral taxa (Pratchett 2013): *Acropora,*
173 *Galaxia, Fungia, Pavona, Montipora, Porites, Pocillopora, Echinopora,* and

174 *Platygyra)* from 90 - 120 replicate photo-quadrats in each of 6 depth bins at 0-5 m, 5-
175 10 m, 10-15 m, 15-20 m, 20-25 m and 25-30 m on one reef (Christine's Reef). We used
176 Coral Point Count with Excel extensions (Kohler and Gill 2006) to record the benthic
177 component under each of six random points within each quadrat ($\geq$ 540 points per
178 depth).
179
180 *Feeding Observations*
181 To assess patterns in feeding ecology, divers followed focal fish for 3 minutes at a
182 distance of ~ 2-3 m and recorded the total number of bites, and the minimum and
183 maximum depth of the observation period. We quantified overall feeding effort by
184 recording bite rates of individuals of both species (*C. baronessa* total n. obs. = 344*, C.*
185 *octofasciatus* total n. obs. = 107) pooled across all hard coral types on six reefs (see
186 suplemental figure S2). Within a subset of these observations (from random depths
187 between 0 and 30m on three reefs), we also recorded the number of bites targeted on
188 each of 37 coral genera (See supplemental Table S1) (*C. baronessa* n. obs = 276*, C.*
189 *octofasciatus* n. obs = 90*).* There was some replication among feeding observations
190 within known monogamous and territorial feeding pairs, resulting in possible pseudo-
191 replication among this subset of observations, which was accounted for in our analyses
192 (See *Data analysis* below). There were no temporal patterns in sampling among depths.
193
194 *Feeding selectivity*
195 The level of selective feeding on *Acoropora* by both species was calculated across all
196 depths and within each 5m depth bin on the focal reef, *Christine's reef* (Suplemental
197 figure S2) using Manly resource selection ratios (Manly et al. 2002). Selectivity was

198 tested by comparing observed and expected bite frequencies on each prey genera based
199 on genera abundance at each depth using chi-squared tests.
200
201 *Nutritional quality of corals*
202 To identify changes in the nutritional quality of corals across depths, we collected a
203 fragment (~7-10 cm) from replicate colonies of two commonly targeted *Acropora*
204 morphologies (tabular; n = 30 and hispidose; n = 37) between 0 m and 40 m depths
205 (Suplemental figure S2). Hispidose colony samples were ground in a mortar and pestle,
206 dehydrated then decalcified using 1M HCL prior to freeze-drying. Tissue from tabular
207 colonies (separate collection) was removed from the skeleton within individual
208 collection bags using an air pick and the resultant slurry collected in vials, dehydrated,
209 and frozen. All samples were dehydrated for ~48 hours at ~55°C then stored in a freezer
210 and freeze-dried prior to lipid extraction. Total lipids were extracted from dried tissue
211 samples using a dichloromethane:methanol solvent protocol (see supplemental
212 methods) and were recorded as proportional dry-weight. Again, there were no temporal
213 patterns in sampling among depths.
214
215 *Trophic carbon pathways of corals and fishes*
216 Depth-related shifts in trophic position and the carbon pathways supporting coral prey
217 were analyzed using bulk stable isotope analyses (SIA_B) of tissue samples from six
218 shallow *Acropora* colonies (0 - 5 m) and four deeper colonies (30 - 40 m). Decalcified,
219 dried, and homogenized non-lipid extracted samples were combusted and analyzed for
220 $\delta^{13}C$ and $\delta^{15}N$ isotope values on a Costech elemental analyzer coupled to a
221 ThermoFinnigan Delta-V gas source isotope-ratio-monitoring mass spectrometer (EA-
222 IRMS). Stable isotope results are reported using standard delta (δ) notation in per mil

223 (‰) relative to standards Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for
224 nitrogen. Reproducibility of lab standards was ± 0.1 ‰ and ± 0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$,
225 respectively.
226
227 To examine the food-web baseline carbon sources utilized by corals and coral-feeding
228 butterflyfishes, we used compound-specific isotope analyses of amino acids (CSIA-
229 AA) from *Chaetodon baronessa* white muscle tissue (n = 5 fish per depth) and lipid-
230 extracted coral tissue (n = 6 colonies per depth) from shallow (0 - 5 m) and deeper
231 depths (30 - 40 m) on the focal reef (Suplemental figure S2). Upper and lower depth
232 boundaries were determined for all sampled fish during previous territorial
233 observations (MacDonald et al. 2018a). Territories of shallow fish were wholly in ≤ 5
234 m depth, deeper fish were wholly ≥ 20 m (max = 40 m) depths. All fish and coral-tissue
235 samples were dried, homogenized, and acid hydrolyzed prior to derivatization to
236 trifluoroacetyl/isopropyl esters (*sensu* McMahon et al. 2018). Derivatized amino acids
237 were analyzed on a Thermo Trace Ultra gas chromatograph coupled to a Finnegan
238 MAT Delta^{Plus} XL GC-IRMS. Standardization of runs was achieved using intermittent
239 pulses of a CO_2 reference gas of known isotopic value and internal nor-Leucine
240 standards. All CSIA-AA samples were analyzed in triplicate along with amino acids
241 standards of known isotopic composition (Sigma-Aldrich Co.). The estimate of full
242 protocol reproducibility was ± 0.7‰.
243
244 To quantify the relative contribution of carbon sources to shallow and deeper
245 populations of *C. baronessa*, we used an amino acid carbon isotope fingerprinting
246 approach (e.g., Larson et al. 2013, McMahon et al. 2015, 2016). We used $\delta^{13}C$ values
247 from five essential amino acids (threonine, isoleucine, valine, phenylalanine, and

leucine) to identify unique isotopic signatures for three potentially important source end-members to fish diets; (i) local shallow and deep-resident *Acropora* coral colonies (collected in this study), (ii) water column phytoplankton (literature values – McMahon et al. 2016), (iii) microbially reprocessed detritus (literature values – McMahon et al. 2016) (Supplemental Table S2). In this study, we refer to "coral carbon" as the internally-derived, zooxanthellic carbon source, distinct from the externally-derived water column phytoplankton from heterotrophic feeding. To compare the essential amino acid fingerprints of source end-members from literature data to the corals and butterflyfish in this study, we examined essential amino acid $\delta^{13}C$ values normalized to the mean of all five essential AAs for each sample. Numerous in-situ and laboratory studies (e.g., Larsen et al. 2013, 2015, Schiff et al. 2014, McMahon et al. 2015, 2016) demonstrate that normalized essential amino acid $\delta^{13}C$ fingerprints provide a diagnostic isotope pattern reflective of the evolutionarily conserved enzymatic pathways of amino acid synthesis among primary producer sources, which are independent of the myriad of environmental conditions affecting bulk $\delta^{13}C$ values across large environmental gradients and among geographic locations (e.g. Heikoop et al. 2000). In addition, source end-member fingerprints are preserved, essentially unchanged, across trophic transfers (McMahon et al. 2010). As such, the normalized essential amino acid $\delta^{13}C$ fingerprints of literature source end-members are robust, faithful proxies of the identity of major carbon sources relevant in this study, regardless of the exact location and growing conditions of the end-members. Greater detail of this established justification is provided in the supplemental material.

Data Analysis

All analyses used R (R Core Team 2016). Acceptable dispersion parameters and homogeneity of variance in residuals were confirmed for all models presented. Final models were tested against other potential models with alternative transformations or distributions, as appropriate. Final models had the lowest Akaike's Information Criterion score (≥ 2 points difference) in *MuMIn* (Barton 2016).

Depth-related variation in total bite rates was tested in each species using negative binomial general linear mixed effect models (glmm). *Total bites* per observation was modeled against median observation *depth* in *lme4* (Bates et al. 2014). *Reef* and known *individual* fish were included as nested random effects. Depth-related variation in the mean proportion of bites on key coral prey genera were analysed among discrete 5m *depth* bins (min and max depth of observations completely within predetermined 5 m depth bins) for each species using glmms on square-root transformed proportional *bite* data and Gaussian distributions (AICc lower than binomial models), with *individual* fish as a random effect. Pairwise comparisons of differences between depths were tested using Tukey's adjusted paired t-tests using *glht* in *multcomp* (Hothorn et al. 2017).

Depth patterns in dietary niche and coral prey composition

Dietary niche breadth was calculated on the total number of bites per coral genera within each 5 m depth-bin and across all depths for both species using coral generic richness and a standardized Levins' index using *pop.diet* in *RInSp* (Zaccarelli et al. 2013). Niche dietary overlap and variance were calculated for each species across all depths and among 5 m depth bins using the Pianka-modification of the MacArthur-Levin's niche overlap index in *EcoSimR* (Gotelli et al. 2015).

298

299 *Depth patterns in the carbon pathways of corals and fishes.*

300 Differences in bulk $\delta^{13}C$ and $\delta^{15}N$ values in between shallow and deeper corals were
301 tested using Welch's t-tests. To quantify the relative contribution of carbon sources to
302 shallow and deep populations of *C. baronessa*, we used Separate Baysean mixing
303 models for each population using *siarsolomcmcv4* (Parnell et al. 2010) within *SIAR*,
304 and a small non-zero trophic discrimination factor of 0.1 ± 0.1‰. The mean model
305 output variance was 7 ± 4%. We tested for statistical significance in depth-related
306 differences in carbon-source contributions to fish tissue using a glmm of a randomized
307 dataset comprised of 1000 values for each individual based on means and standard
308 deviations produced by *SIAR* results and with *individual* fish used as a random variable.

309

310 **Results:**

311

312 **Depth patterns in overall resource quantity and feeding effort**

313

314 *Acropora* availability declined with depth throughout Kimbe Bay, declining by >50 %
315 from the shallowest 5 m (17.0 ± 1.9 SE %) to 30 m (8.3 ± 1.8 %) ($z = -3.25$, $p = 0.006$)
316 (Fig.1a). However, the availability of all potential coral food sources to coral-feeding
317 fishes (total hard-coral cover) was consistently high at all depths ($F_{1,3} = 2.74$, $p = 0.20$),
318 range: 49 - 62 %) (Fig. 1a). Overall feeding rates on all hard coral types did not decline
319 with depth in either species. (*C. baronessa*, $z = 0.64$, $p = 0.52$; *C. octofasciatus*, $z =$
320 1.15, $p = 0.25$) (Fig. 1 b,c).

321

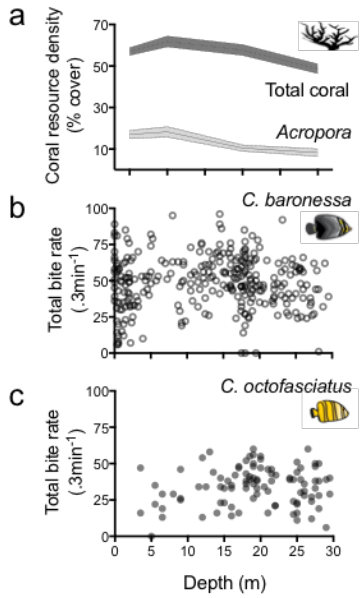

Figure 1: (a) The mean cover (± 95% CI) of total hard coral and *Acropora* coral resources along a depth gradient from 0 to 30 m in Kimbe Bay, PNG; (b) The total bite rate on all corals along the same depth gradient for the 'shallow-specialist' butterflyfish *Chaetodon baronessa* (grey fish); and (c) the total bite rate on all corals along the depth gradient for the 'deep-generalist' butterflyfish *C. octofasciatus* (yellow fish). Each point represents the total bites observed during a three-minute feeding observation. Data points are semi-translucent.

Depth-related variation in resource composition and feeding flexibility

Changes in available coral resource types

Total hard coral cover on the focal reef was high throughout the gradient and increased from 55 ± 2.1 % at 0 - 5 m to a peak of 73 ± 2.4 % at 10 – 15 m ($t = 4.84$, $p < 0.001$), before declining to 39 ± 2.6 % at 25-30 m ($t = -7.58$, $p < 0.001$) (Fig. 2a). *Acropora* cover declined monotonically ($F_{5,674} = 10.91$, $p < 0.001$) (Fig. 2b), decreasing fourfold

339 from 22 ± 2.0 % at 0 - 5 m to 5 ± 1.5 % at 25 – 30m ($t = -6.35$, $p < 0.001$) (Fig 2a).
340 *Porites* cover closely followed total hard coral cover, doubling from 15 ± 1.3 % cover
341 at 0 - 5 m to 31 ± 2.6 % at 10 – 15 m ($t = 5.97$, $p < 0.001$), then declining to 11 ± 1.1 %
342 at 25 – 30 m ($t = -6.25$, $p < 0.001$). All other coral genera were less abundant and
343 showed variable patterns with depth (Fig 2a).
344
345 *Depth-related changes in corallivore diets*
346 The dietary niche breadth of the shallow-specialist, *C. baronessa*, was narrow overall
347 and remained highly specialised along the gradient (Fig. 2 c,e). Overal niche breadth
348 was 0.07, and the species fed on a total of 18 coral genera across the gradient. Niche
349 overlap among all depths was 0.95, and neither niche breadth ($F_{1,4} = 0.467$, $p = 0.53$)
350 nor the total number of dietary genera ($F_{1,4} = 0.233$, $p = 0.65$) increased with depth.
351 There was a small increasing trend in niche breadth between 5-10 m (0.01) and 20-25
352 m (0.09) (Fig 2e). However, niche breadth was highest in the shallowest depth (Levins'
353 index = 0.21), where the most dietary genera (15) were also utilized. The lowest overlap
354 in the dietary niche of the shallow-specialist population was 0.86, and occurred between
355 0-5 m and 25-30 m depths.
356
357 In contrast, the deep-generalist *C. octofasciatus* had a broad overall dietary niche (niche
358 breadth = 0.23, 36 genera), low niche overlap between depths (0.36), and an increasing
359 breadth of utilized genera from 7 genera at 0-5 m to 25 genera at 25-30 m ($F_{1,4} = 8.41$,
360 $p = 0.044$, $R^2 = 0.597$) (Fig. 2 d,f). The dietary niche realized by the deep-generalist did
361 not increase significantly with increasing depth ($F_{1,4} = 1.41$, $p = 0.30$, $R^2 = 0.597$) (Fig.
362 2f). Instead, a general increase occurred between 5 m (0.12) and 30 m (0.26), but was
363 punctuated by 65 - 75 % decrease in niche at 15 - 20 m (0.07) compared to other depths.

There was high variation in dietary overlap between depths for the deep-generalist (0.229 – 0.895) and no clear depth-related patterns in this variation.

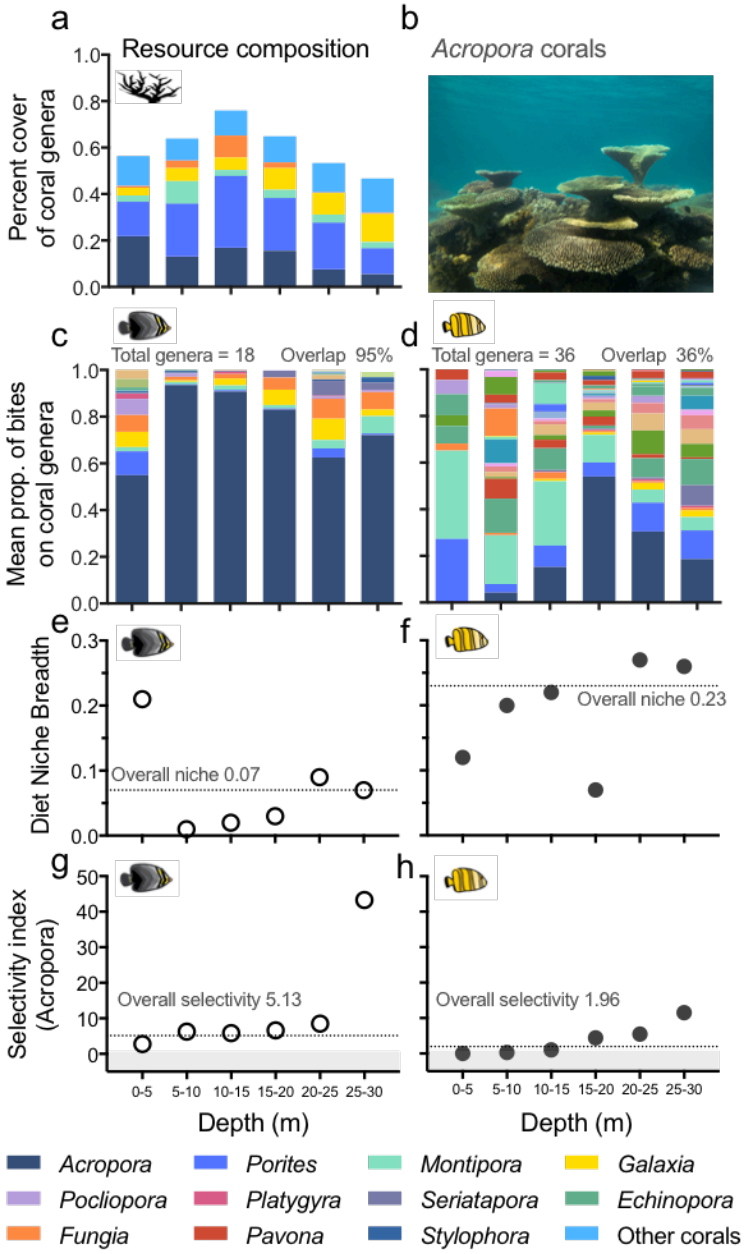

Figure 2: Depth-related variation in resource availability (a), diet (c-f), niche breadth (e-f) and selectivity (g, h) of a shallow-specialist (*Chaetodon baronessa*) and deep-generalist (*C. octofasciatus*) corallivore, along a coral-reef depth gradient. (a) The percent cover of primary coral genera within each 5 m depth-bin on the focal reef (total bar height = total cover). (b) A stand of *Acropora* colonies, the preferred dietary coral of many butterflyfish species including *Chaetodon baronessa*. (c & d) The proportional

number of bites on primary dietary coral genera. (e & f) The breadth of dietary niche; a full list of taxa is provided in Supplemental table S1. (g & h) Dietary selection for the preferred coral genus *Acropora.* Dotted lines in e - h indicate overall metrics across all depths. In g & h, values < 1 (greyed-out area) indicate avoidance of *Acropora*, and values > 1 indicate positive selection for the genus. Photo credit: C. MacDonald.

Depth-related variation in the utilization and selectivity of preferred resources

Proportional foraging was higher on *Acropora* than on any other coral genus for both species and did not decrease uniformly with depth among either species (Fig. 2 c,d). However, some non-linear differences among depths were evident: *C. baronessa* fed predominantly on *Acropora* (75 % of all bites) across all depths (Fig. 2c, Supplemental Figure S3), but utilized the genus approximately 1.5 - 2 times less in the shallowest depth (0 - 5 m, ~ 45% of bites), with no significant difference among depths > 5 m (all comparisons, $p > 0.10$). *Chaetodon octofasciatus* took fewer bites from *Acropora* overall (31 % of all bites) and fed on *Acropora* more than any other coral genera at depths > 15 m (Fig. 2 d, Supplemental Figure S3). *Chaetodon octofasciatus* did not feed on *Acropora* at 0 - 5 m and took a higher proportion of bites on *Acropora* at 15 - 20 m (55 %) than at 5 - 10 m (Tukey's; $z = -2.90$, $p = 0.039$), but not at other depths (all comparisons, $p > 0.10$).

Overall, both species fed on *Acropora* colonies more than expected given *Acropora* availability (Table 1, Fig. 2 g,h). However, selective feeding increased with depth in both species despite the decline in *Acropora* abundance. *Acropora* selection by *C. baronessa* increased linearly between 0 - 5 m (selectivity ratio = 2.77) and 20 - 25 m

400 (selectivity ratio = 8.48) ($F_{1,3}$ = 12.79, p = 0.034, R^2 = 0.75), then more than quadrupled
401 between 20 - 25 m and 25 - 30 m to the point where the proportion of bites targeting
402 *Acropora* was 43 times greater than its proportional cover (selectivity ratio; 43.3) (Fig.
403 2g, Table 1). Selective feeding on *Acropora* by *C. octofasciatus* also increased linearly
404 with depth ($F_{1,4}$ = 24.72, p = 0.007, R^2 = 0.83), but showed a different pattern to *C.*
405 *baronessa*: *C. octofasciatus* avoided feeding on *Acropora* colonies between 0 - 10 m,
406 fed in proportion to availability at 10 - 15 m, and selectively fed on them at depths >
407 15m (all depths; p < 0.001) (Fig. 2h).
408
409 **Compensatory mechanisms of energy acquisition**
410
411 The total lipid content (energy availability) in *Acropora* coral tissue did not decline
412 with depth (z = -0.42, p = 0.67) (Fig. 3a). However, there were indications of
413 compensatory energy acquisition in both *Acropora* (Fig. 3b) and deeper resident fish
414 (Fig 3c). Tissue from deeper *Acropora* colonies had lower bulk $\delta^{13}C$ values than
415 shallow-reef *Acropora* (t = 10.16, p = 0.001) (Fig. 3b), as did the compound specific
416 $\delta^{13}C$ of essential amino acids within the *Acropora* tissues (Fig. 3c). Bulk $\delta^{15}N$ values
417 in *Acropora* correspondingly increased with depth (t = -12.52, p < 0.001) (Fig 3b).
418
419 The $\delta^{13}C$ values of essential amino acids within *C. baronessa* muscle tissue were also
420 lower among deeper-reef residents (Fig 3c, Supplimental Table S3). CSIA-AA-based
421 mixing models of relative source end-member carbon contributions to *C. baronessa*
422 muscle tissue further supported differentiation in the dietary carbon pathways of
423 shallow-reef and deeper-reef butterflyfish populations (Fig 3d). As expected, coral-
424 fixed carbon was the dominant carbon source supporting *C. baronessa* overall (79 ±

13%). However, the relative contribution of coral-sourced carbon to the food web supporting *C. baronessa* decreased by a 25% between depths (Shallow 90 ± 2% (SD); Deep: 67 ± 5%). Concurrently, the relative contribution of water-column derived planktonic carbon increased substantially among deeper-resident fish (Shallow: 7 ± 2%; Deep: 27 ± 4%) (Fig. 3d). In both populations, microbially-reprocessed detritus made up a relatively small contribution of total carbon to *C. baronessa* (Deeper: 6 ± 1%; Shallow: 3 ± 1%).

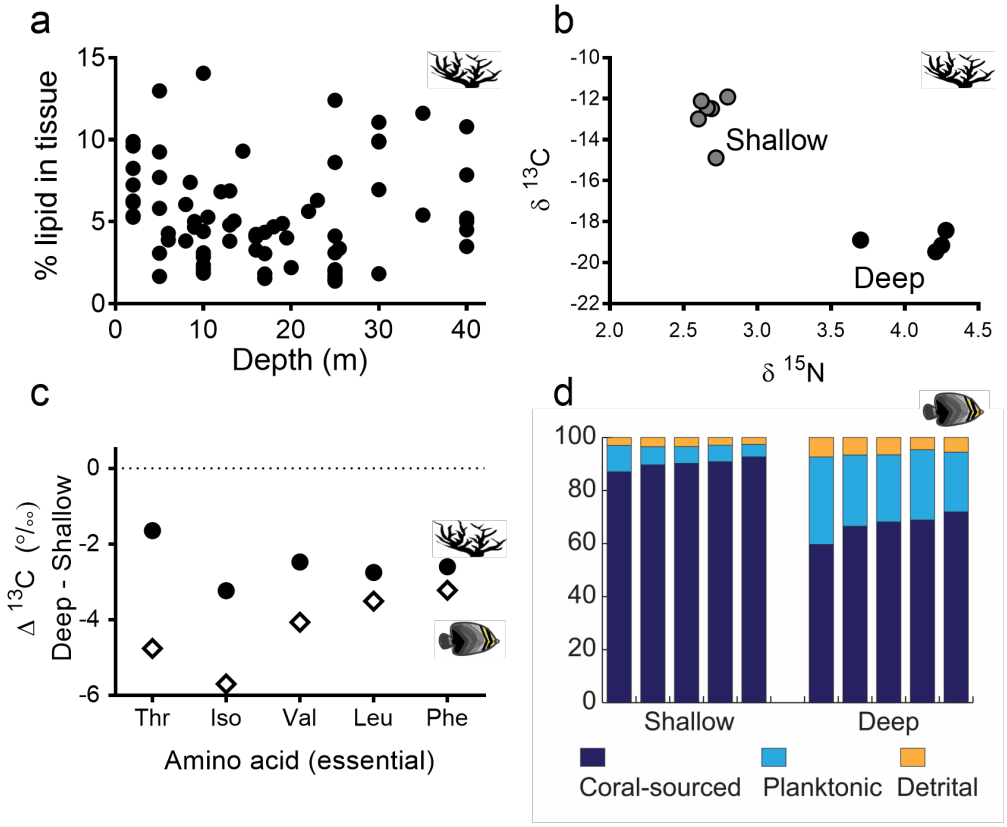

Figure 3: (a) The proportional lipid content of *Acropora* tissue along a depth gradient from 0 – 40 m. (b) Differences in occupation of isotopic space between shallow (grey) and deep (black) *Acropora* corals. (c) Altered carbon pathway signals in the essential amino acids of *Acropora* colonies (dots) and *Chaetodon baronessa* individuals (diamonds) on the deeper reef. (d) Relative carbon contributions from coral, water

column plankton, and microbially reprocessed detritus to *Chaetodon baronessa* residents from the shallow (0 – 5 m) and deep-reef (20 – 40 m).

Table 1: Dietary niche breadth and overlap between 5 m depth bins for two *Chaetodon* species between 0 m and 30 m. (0 = no dietary overlap, 1 = full dietary overlap). Niche overlap is based on Levin's index and selectivity on Manly's resource selction ratios.

Sp.	Depth (m)	No. obs	No. bites	Niche overlap						Prey selectivity ratios and evidence for selection							
				All	0-5	5-10	10-15	15-20	20-25	*Acro.*	*p*	*Mont.*	*p*	*Porit.*	*p*	*Echin.*	*p*
C. baronessa	All depths	159	3309	0.952						5.13	***	0.55	***	0.14	***	0.78	*
	0-5	48	946	-	1					2.77	***	0.77	NS	0.70	***	3.50	***
	5-10	10	314	-	0.933	1				6.27	***	0.11	***	0.02	***	0.39	*
	10-15	18	451	-	0.923	0.992	1			5.83	***	0.81	NS	0.02	***	0.74	NS
	15-20	58	1101	-	0.925	0.996	0.991	1		6.60	***	0.45	***	0.01	***	0.56	***
	20-25	11	368	-	0.925	0.996	0.988	0.998	1	8.48	***	2.00	NS	0.34	***	0.73	NS
	25-30	14	129	-	0.860	0.928	0.940	0.925	0.947	43.3	***	2.62	***	0.06	***	0.40	**
C. octofasciatus	All depths	79	2395	0.360						1.96	***	2.97	***	0.42	***	1.08	NS
	0-5	3	63	-	1					0.00	***	13.63	***	1.95	NS	7.27	NS
	5-10	11	151	-	0.726	1				0.29	***	2.22	***	0.17	***	0.90	NS
	10-15	13	272	-	0.804	0.841	1			1.02	NS	10.69	***	0.31	***	1.43	NS
	15-20	18	768	-	0.229	0.278	0.568	1		4.43	***	3.31	***	0.27	***	0.57	NS
	20-25	13	417	-	0.376	0.332	0.567	0.893	1	5.46	***	1.59	NS	0.62	**	0.95	NS
	25-30	21	724	-	0.468	0.438	0.597	0.728	0.895	11.5	***		**	1.15	NS	0.50	**

Obs = observation, *Acro. = Acropora, Mont. = Montipora, Porit. = Porites, Echin. = Echinopora.* NS = Non-significant.

Discussion:

Counter to expectations, our results demonstrate that a combination of: 1) more intensive feeding on less available preferred corals (specialist strategy); 2) dietary flexibility (generalist strategy); and, 3) compensatory energy acquisition by deeper-reef corals and/or fish, work together to provide the required nutrition required to facilitate broad depth distributions in coral-obligate butterflyfish species. We have previously demonstrated that neither body condition nor reproductive potential decline with depth in either of our focal fish species (MacDonald et al. 2018a). Therfore, costs at the deep range margins for these coral-obligate species may not be as severe as previously expected.

458

459 The dietary strategies reported for *C. baronessa* and *C. octofasciatus* in shallow water
460 were largely consistent along the depth gradient. The specialist remained specialized,
461 while the generalist became more generalized with increasing depth. Unexpectedly, the
462 relative feeding effort (selectivity) targeting *Acropora* increased with depth for both
463 species. For the specialist, this is likely related to a continued reliance on *Acropora*, but
464 for the generalist may be related to competitive release of the preferred resource at
465 deeper depths, due to decreased abundance of the dominant *C. baronessa* (Blowes et
466 al. 2013, MacDonald et al. 2016). Specialist dietary strategies incur greater risk due to
467 decreased flexiblity and limited resource distributions, therefore species with broad
468 depth-distributions could be expected to exhibit generalist diets, while coral-specialists
469 should be limited to shallow waters (e.g. Bridge et al. 2016). However, we demonstrate
470 here that broad depth ranges in coral-specialist species can be supported via contrasting
471 specialist and generalist dietary strategies. Increased dietary breadth with depth in *C.*
472 *octofasciatus* here followed theoretical expectations and empirical observations in non-
473 coral-associated generalist species (Goldstein et al. 2017). However, maintained dietary
474 specialization along broad depth gradients (*C. baronessa*) has not been previously
475 recorded in coral-reef fishes and demonstrates that dietary flexibility is not necessarily
476 a prerequisite for broad depth distributions. Further, similar non-depth-dependence in
477 degree of coral microhabitat specialization is evident among microhabitat specialist and
478 generalist damselfishes (Jankowski et al. 2015, MacDonald et al. 2018b). This suggests
479 a potential generalisation of non-depth-dependence in niche specialization across
480 multiple functional spaces for coral-specialist reef fishes.

481

Identifying the carbon sources supporting consumer production can aid understanding or allow predictions of consumer responses to changes in environment and food web structure. Not surprisingly, coral-fixed carbon sources dominated *C. baronessa's* overall dietary makeup, according to both in-situ feeding observations and amino acid isotope fingerprinting of muscle tissue. However, despite maintained specialization within overt coral feeding behaviours, our results unexpectedly indicate that deeper *C. baronessa* occupy a different nutritional niche than their shallow-water counterparts, within tens of meters. Relative muscle-tissue carbon sources shifted from 90% to 67% coral contributions within 30m depth and demonstrated a corresponding four-fold increase in plankton sourced carbon at deeper depths. Cryptic supplemental feeding by *C. baronessa* on non-coral hosts may therefore provide dietary compenstation at depth and greater potential capacity to respond to coral loss than previously assumed. This is surprising because *C. baronessa* is widley considered an obligate corallivore and supplemental feeding on non-coral diets has not been observed previously (Pratchett et al. 2013), nor within this study.

An alternative hypothesis to cryptic supplemental feeding by *C. baronessa* at depth is that increased water-column derived planktonic carbon in deeper water fish was routed through corals, via depth-related increases in coral heterotrophy. A couple of lines of evidence support this hypothesis. Under experimentally reduced light conditions, corals can exhibit 30% - 90% reductions in lipid storage, which is burned for compensatory energy, with the smallest lipid declines occuring in species capable of heterotrophic substitution (Anthony and Fabricius 2000, Hoogenboom et al. 2010). Contrary to expectation, the coral lipid content of small-polyped *Acropora* here, a taxon considered highly dependent on autotrophy, did not decline with depth. At the same time, both

507 SIA_b and CSIA-AA data show marked decreases in $\delta^{13}C$ values with depth, which
508 cannot be ascribed to changes in lipid utilization. As per previous SIA_b studies
509 (Muscatine et al. 1989, Risk et al. 1994), we hypothesize that these $\delta^{13}C$ data indicate
510 increased coral heterotrophy, in this case with depth. Whilst direct comparisons of bulk
511 $\delta^{13}C$ isotope values should be used with caution, the values we observed in deep-water
512 specimens were similar to entirely heterotrophic large-polyped corals (*Tubastrea*
513 *coccinea;* -20.7 ‰ (Land et al. 1977), and to oceanic POC/DOC (-18 ‰ to -24 ‰),
514 while shallow water values matched those typical of autotrophic corals (-11 ‰ to -14
515 ‰) (Muscatine et al. 1989, Heikoop et al. 2000). As such, the hypothesized
516 compensatory coral heterotrophy may offset coral energy requirements at depth,
517 allowing corals to maintain lipid stores critical to energy resilience (Grottoli et al.
518 2006). If true, the robustness of our CSIA-AA results bolster interpretations from bulk
519 $\delta^{13}C$ studies and provide strong evidence for depth-mediated metabolic uptake of
520 heterotrophically-sourced energy in corals and a subsequent trophic transfer into coral
521 consumers, which has not previously been shown.
522
523 Enrichment of an organism's bulk $\delta^{15}N$ values generally indicates increases in trophic
524 position (e.g., Minagawa et al. 1984). Whilst relatively small, enriched $\delta^{15}N$ values in
525 deeper corals here may further support our trophic transfer hypothesis. It should be
526 noted that oceanographic variations such as internal waves and upwellings can result in
527 periodic N pulses (Sammarco et al. 1999, Heikoop et al. 2000, Leichter et al. 2003),
528 that have been linked to bulk $\delta^{15}N$ enrichment among deeper-water algae and greater
529 copeopod densities with depth (Leichter et al. 1998), as well as in variable bulk $\delta^{15}N$
530 of shallow-water corals among shelf positions (Sammarco et al. 1999) and broad
531 geographic locations (Heikoop et al. 2000). It is not known whether similar processes

532 operate differentially within tens of meters of depth in Kimbe Bay. Therefore, we
533 cannot rule-out an additional role of depth-related variation in the nutritional-content
534 of heterotrophic food sources as a potential mechanism for the propossed increases in
535 heterotrophic carbon uptake. Both possibilities, however, suggest that multiple
536 mechanisms may act to buffer the marginality of deep reef habitats for specialist species
537 vulnerable to shallow-water habitat loss.
538
539 The results here suggest increased coral heterotrophy and/or substitute feeding on
540 plankton may additionally buffer 'coral-obligate' fish from depth-related declines in
541 the availability and hypothesized declines in nutritional quality of preferred corals.
542 Similar depth related nutiritional shifts are evident in the isotopic space occupied by
543 less coral associated and more generalist fish taxon and feeding guilds (Bradley et al.
544 2016, Goldstein et al. 2017). Together, these data suggest significantly altered energy
545 pathways may be a key mechanism supporting a variety of consumers on deeper reefs.
546
547 Increasing vulnerability to anthropogenic impacts at range cores and consequential
548 range displacements, particularly among resource specialists, has increased the
549 necessity to assess ecological mechanisms that support potentially viabile spatial
550 refuges, many of which will occur at current range margins (Keppel et al. 2012). Our
551 data show variable and potentially multi-trophic functional responses can act to buffer
552 costs and bolster refuge potentials associated with dwelling at range peripheries (here,
553 deeper reef habitats), even among taxa with contrasting functional strategies.
554
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Supplemental Materials for:

Alternative functional strategies and altered carbon pathways facilitate broad depth ranges in corals and coral-obligate reef fishes

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Table S1: The proportion of bites taken from each coral taxon within 5m depth bins along a gradient from 0 – 30 m.

Coral taxa	*Chaetodon baronessa*							*Chaetodon octofasciatus*						
	Depth bin (m)							Depth bin (m)						
	All depths	0-5	5-10	10-15	15-20	20-25	25-30	All Depths	0-5	5-10	10-15	15-20	20-25	25-30
Acropora	0.75	0.57	0.94	0.91	0.83	0.62	0.72	0.31	-	0.04	0.18	0.55	0.31	0.19
Galaxia	0.06	0.06	0.01	0.03	0.06	0.08	0.02	0.02	-	-	<0.01	0.01	0.03	0.03
Fungia	0.06	0.08	0.02	0.02	0.05	0.09	0.09	0.01	0.03	-	0.03	0.01	0.01	0.01
Seriatapora	0.02	0	0	0.01	0.03	0.07	0.03	0.03	-	-	0.01	<0.01	0.01	0.09
Montipora	0.03	0.02	0.01	0.02	0.02	0.04	0.09	0.15	0.4	0.42	0.4	0.12	0.06	0.06
Pocliopora	0.02	0.06	0.02	-	<0.01	0.01	0.01	-	-	-	-	-	-	-
Diploastrea	0.01	0.04	-	-	-	0.02	-	-	-	-	-	-	-	-
Stylophora	0.01	0.01	0.01	-	-	0.01	0.02	<0.01	-	-	-	<0.01	0.01	<0.01
Porites	0.03	0.08	<0.01	0.01	<0.01	0.04	0.01	0.10	0.29	0.03	0.11	0.06	0.12	0.13
Maerulina	0.01	0.01	-	-	-	0.01	-	0.01	-	-	0.01	<0.01	<0.01	0.02
Platygyra	0.01	0.02	-	0.01	-	<0.01	-	0.01	-	-	<0.01	0.01	0.01	0.01
Echinata	<0.01	-	-	-	-	<0.01	0.03	-	-	-	-	-	-	-
Goniastrea	0.01	0.04	-	-	<0.01	-	-	0.05	0.05	-	<0.01	0.03	0.1	0.06
Pavona	<0.01	<0.01	-	-	-	-	-	0.02	-	-	0.01	0.04	0.02	0.01
Favities	-	-	-	-	-	-	-	0.02	0.1	-	-	<0.01	0.04	0.03
Anacropora	<0.01	-	-	<0.01	-	-	-	0	-	-	-	-	0	<0.01
Echinopora	-	-	-	-	-	-	-	0.09	0.08	0.26	0.12	0.01	0.08	0.12
Turbinaria	-	-	-	-	-	-	-	0	-	-	-	-	-	0.01
Mycedium	-	-	-	-	-	-	-	0.02	-	-	-	0.01	-	0.06
Pachyseris	-	-	-	-	-	-	-	0.05	-	0.05	-	0.04	0.07	0.06
Asteopora	-	-	-	-	-	-	-	0.01	-	-	-	0.01	0.03	<0.01
Oxyopora	-	-	-	-	-	-	-	0.02	-	-	0.11	0.01	<0.01	0.01
Leptoseris	-	-	-	-	-	-	-	0.03	-	0.01	-	0.01	0.05	0.06
Physogyra	-	-	-	-	-	-	-	<0.01	-	-	-	-	0.01	-
Hydnophora	<0.01	<0.01	-	-	-	-	-	<0.01	-	-	-	0.01	-	-
Montastrea	-	-	-	-	-	-	-	0.01	0.06	0.03	-	<0.01	<0.01	0.01
Psammocora	-	-	-	-	-	-	-	<0.01	-	-	<0.01	-	<0.01	-
Trathyphilia	-	-	-	-	-	-	-	0.01	-	-	-	0.01	-	-
Acanthastria	-	-	-	-	-	-	-	0.01	-	-	-	0.02	-	-
Coscinaraea	-	-	-	-	-	-	-	<0.01	-	-	-	-	0.02	-
Pectinia	-	-	-	-	-	-	-	0.02	-	0.15	0.01	0.02	-	0.01
Gardenerosis	<0.01	<0.01	-	-	<0.01	-	-	<0.01	-	-	-	-	0.01	-
Milipora	-	-	-	-	-	-	-	<0.01	-	0.02	-	-	-	-
Halomitra	-	-	-	-	-	-	-	<0.01	<0.01	-	-	-	-	-
Lobophylia	-	-	-	-	-	-	-	<0.01	<0.01	-	-	-	-	-
Herpolitha	-	-	-	-	-	-	-	0.003	0.02	-	-	-	-	-
Other encrusting	-	-	-	-	-	-	-	<0.01	-	-	-	0.01	<0.01	0.01
Other branching	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-
Other massive	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other laminar	<0.01	<0.01	-	-	-	-	-	-	-	-	-	-	-	-
Dead coral	-	-	-	-	-	-	-	<0.01	-	-	-	0.01	-	-

Supplemental Methods:

Lipid extraction protocol

Freeze dried coral tissue samples (see main methods), were weighed to the nearest 0.000g. 2ml of a dichloromethane : methanol (2:1) solvent was added to each sample and mixed for 10 minutes in a Sonicator. After cooling, the sample/solvent mix was filtered through solvent extracted cotton-stuffed, glass Pasteur pipettes using pressure from a hand bulb. An additional 1ml of dichloromethane : methanol solvent was passed through the filter to wash all of the lipid solvent solution into collection vials. 3.5ml of sample wash [KCl 0.44% in H_20

(3): Methanol (1)] was added and left overnight for lipids to fall out of solution. The top layer of samples (non-lipid) were removed using a Pasteur pipette with bulb. Lipid samples were recovered into pre-weighed and labelled glass vials using a 1.0ml glass syringe and the solvent was evaporated in a nitrogen evaporator. Total lipids were quantified by re-weighing pre-weighed vials to the nearest 0.000g, now containing lipids.

Complete methods and justification for compound specific stable isotope protocol

To examine the relative contribution of carbon source end-members to corals and coral-feeding butterflyfishes, we used an amino acid carbon isotope fingerprinting approach (McMahon et al. 2015, 2016) within a fully Bayesian stable isotope mixing model (sensu Ward et al. 2010) using the *SIAR* package (Parnell et al. 2010; R development core team 2013, ver. 3.0.2). We used three data files to parameterize our mixing model: 1) consumer data consisting of $\delta^{13}C$ values for five essential amino acids (threonine, isoleucine, valine, leucine, phenylalanine) for individual coral or butterflyfish (separate models), 2) source end-member essential amino acid $\delta^{13}C$ fingerprints (see description below), and 3) Trophic discrimination factors for the five essential amino acids (0.1 ± 0.1; McMahon et al. 2010). In SIAR, we ran 500,000 iterations with an initial discard of the first 50,000 iterations as burn-in. By using $\delta^{13}C_{EAA}$ values within the Bayesian isotope mixing model, we avoid the major issue that plagues poorly resolved dual isotope approaches in multi-end-member systems (Fry 2013; Brett 2014): underdetermined mixing, and complications of variable and poorly characterized trophic fractionation (Bond and Diamond 2011).

We characterized unique amino acids isotope fingerprints (multi-variate patterns in relative $\delta^{13}C$ among essential amino acids) for three potentially important source end-members to *Chaetodon baronessa*: autotrophic coral carbon (zooxanthellae-proxy), herbivorous zooplankton carbon (water column phytoplankton proxy), and detritivorous sea cucumber carbon (microbially-reprocessed detritus proxy). The source end-member data (Table S2) pulled from a relevant subset of molecular-isotopic training data sets from McMahon et al. (2016) (see justification for using literature data below). McMahon et al. (2016) collected staghorn coral, *Acropora pharaonis*, that is targeted by coral-eating butterflyfish (e.g., Berumen and Pratchett 2008) to represent carbon fixed by autotrophic zooxanthellae. The essential amino acid $\delta^{13}C$ fingerprints of these corals aligned with the essential amino acid $\delta^{13}C$ fingerprints of pure cultures of *Symbiodinium* sp. from Woods Hole Oceanographic Institution, indicating that these corals rely almost exclusively on autotrophically fixed carbon with little to no heterotrophic feeding. As such, we used these corals as proxies for autotrophic coral end-members in our mixing model. McMahon et al. (2016) collected pelagic calanoid copepods that feed on water column phytoplankton as

proxies for water column phytoplankton carbon. They did not use phytoplankton directly because the fast turnover rate of phytoplankton means that their isotope signatures are just a snapshot of the water column baseline signature. Instead, they analyzed zooplankton, which integrate dietary carbon signals over longer time scales more relevant to the turnover rates of butterflyfish. Furthermore, given that essential amino acids show virtually no isotope discrimination between diet and consumer (McMahon et al. 2010), the essential amino acid $\delta^{13}C$ values of pelagic copepods provided a faithful proxy for pelagic phytoplankton. As expected, the essential amino acid $\delta^{13}C$ fingerprints of these coral reef plankton aligned with the fingerprints of water column phytoplankton from the Larsen et al. (2013) dataset. Given the challenges in isolating the detrital end-member, McMahon et al. (2016) selected the detritivorous black sea cucumber, *Holothuria atra*, as a proxy for microbially reprocessed detritus (Moriarty 1982; Uthicke 1999). These detritus-proxy fingerprints aligned with heterotrophic bacteria from the Larsen et al. (2013) dataset. Together, these source end-member essential amino acid $\delta^{13}C$ fingerprints provide a robust data set to reconstruct the relative contribution of source end-members to coral and butterflyfish production.

We focused our analyses on only essential amino acids (threonine, isoleucine, valine, leucine, and phenylalanine) for two reasons: 1) The essential amino acid $\delta^{13}C$ fingerprints represent the sum of the isotopic fractionations associated with individual biosynthetic pathways and associated branch points for each essential amino acid (Hayes 2001; Scott et al. 2006), generating phylogenetically diagnostic amino acid fingerprints of different source end-members (Larsen et al. 2009, 2013). Because essential amino acids have very long and complex biosynthetic pathways (typically >10 independent enzymatic steps), they provide the best potential for lineage-specific isotope effects (*Lehninger 1975; Stephanopoulos et al. 1998*). 2) Essential amino acid $\delta^{13}C$ patterns of source end-members are preserved, essentially unchanged, across trophic transfers (14, McMahon et al. 2010). This is because, while plants, algae, and bacteria can synthesize essential amino acids *de novo,* metazoans have lost the necessary enzymatic capabilities and must acquire essential amino acids directly from their diet with minimal fractionation (Reeds 2000).

In order to compare the essential amino acid fingerprints of our three source end-member groups collected from literature data to the corals and butterflyfish in this study, we examined essential amino acid $\delta^{13}C$ values that were normalized to the mean of all five essential AAs for each sample. As expected, there is strong experimental and field-based evidence that primary producer essential amino acid $\delta^{13}C$ fingerprints are faithful and robust across large environmental gradients in growing conditions and carbon sources that can affect bulk $\delta^{13}C$ values (Larsen et al. 2009, 2013, 2015). This is because the underlying biochemical mechanisms generating unique internally normalized essential amino acid $\delta^{13}C$ fingerprints are driven by major evolutionary diversity in the central synthesis and metabolism of amino acids. For example, Larsen et al. (2013) examined the extent to which

normalized essential amino acid $\delta^{13}C$ fingerprints were affected by environmental conditions by looking at seagrass (*Posidonia oceanica*) and giant kelp communities (*Macrocystis pyrifera*) across a variety of oceanographic and growth conditions (see Larsen et al. 2013 Table S1 for details). For both species, the range in bulk $\delta^{13}C$ values was five- to ten-times greater (2.6‰ and 5.2‰, respectively) than it was for normalized essential amino acids $\delta^{13}C$ (0.4‰ to 0.6‰, respectively). By normalizing the individual $\delta^{13}C_{EAA}$ values to the mean, Larsen et al. (2013) showed that natural variability in $\delta^{13}C$ values of individual amino acids is effectively removed, creating diagnostic fingerprints that were independent of environmental conditions. Larsen et al. (2015) further confirmed this concept with the first directly controlled physiological studies of fidelity in normalized essential amino acid $\delta^{13}C$ fingerprints. This study grew the laboratory-cultured marine diatom, *Thalassiosira weissflogii*, under a wide range of conditions: light, salinity, temperature, and pH. This study showed that normalized essential amino acid $\delta^{13}C$ values remained unmodified despite very large changes in bulk and raw amino acid $\delta^{13}C$ values (>10‰), molar percent abundances of individual amino acids, and total cellular carbon to nitrogen ratios. Together, Larsen et al. (2013, 2015) provide strong evidence that normalized essential amino acid $\delta^{13}C$ fingerprints are diagnostic of the primary producer source rather than the myriad factors affecting bulk $\delta^{13}C$ values, such as carbon availability, growth conditions, and oceanographic conditions. As such, we are confident that the normalized essential amino acid $\delta^{13}C$ fingerprints of literature source end-members are robust, faithful proxies of the identity of major carbon sources relevant in this study, regardless of the exact location and growing conditions of the end-members.

Table S2. Mean (‰ ± SD) essential amino acid $\delta^{13}C$ values of three source end-members (n = 24 individuals for each source end-member) characteristic of potential carbon sources fueling coral and butterflyfish (Literature data from McMahon et al. 2016). Each essential amino acid $\delta^{13}C$ value was normalized to the mean of all essential amino acid $\delta^{13}C$ values within each individual to facilitate comparisons of amino acid "fingerprints" across systems and environmental conditions (sensu Larsen et al. 2015).

End-member	Threonine	Isoleucine	Valine	Leucine	Phenylalanine
Plankton	10.0 ± 1.2	2.8 ± 0.8	-2.3 ± 1.0	-5.8 ± 0.6	-4.7 ± 0.6
Coral	11.7 ± 1.0	5.7 ± 1.2	-6.4 ± 0.6	-7.1 ± 1.1	-3.9 ± 1.3
Detritus	10.4 ± 1.2	-0.6 ± 0.7	-1.6 ± 0.7	-3.2 ± 0.9	-5.1 ± 0.8

Table S3. Essential amino acid $\delta^{13}C$ values (‰) of individual *Acropora spp*. colonies (n = 6 colonies per depth) and individual *Chaetodon baronessa* (n = 5 individuals per depth) form 5m and 40m water depth in Kimbe Bay, Papua New Guinea. Each essential amino acid $\delta^{13}C$ value was normalized to the mean of all essential amino acid $\delta^{13}C$ values within each individual to facilitate comparisons of amino acid "fingerprints" across systems and environmental conditions (sensu Larsen et al. 2015).

		Consumer	Threonine	Isoleucine	Valine	Leucine	Phenylalanine
Acropora	Shallow	AS1	11.3	6.1	-5.3	-7.1	-5.0
		AS2	10.8	5.4	-4.7	-6.0	-5.5
		AS3	12.5	4.4	-5.4	-6.1	-5.4
		AS4	12.6	5.5	-6.0	-5.8	-6.3
		AS5	11.1	5.5	-4.7	-5.8	-6.0
		AS6	11.6	5.3	-4.7	-7.4	-4.8
	Deep	AD1	12.0	5.5	-4.7	-6.6	-6.3
		AD2	11.9	5.0	-5.3	-5.9	-5.6
		AD3	11.5	4.3	-4.6	-6.4	-4.8
		AD4	13.0	5.0	-5.2	-6.6	-6.2
		AD5	13.1	3.5	-4.8	-6.4	-5.4
		AD6	13.9	4.7	-5.8	-7.7	-5.2
Chaetodon baronessa	Shallow	C_barSA	11.7	6.0	-4.4	-7.1	-6.3
		C_barSB	12.4	6.0	-4.6	-7.5	-6.3
		C_barSC	12.6	5.5	-4.2	-7.6	-6.4
		C_barSD	10.7	6.1	-3.5	-7.1	-6.1
		C_barSE	12.2	5.6	-4.7	-7.1	-6.0
	Deep	C_barDA	11.5	3.5	-4.4	-6.5	-4.1
		C_barDB	11.0	4.9	-4.4	-6.2	-5.3
		C_barDC	11.4	4.5	-4.2	-6.4	-5.3
		C_barDD	11.1	4.8	-4.1	-6.8	-5.0
		C_barDE	12.2	4.3	-3.4	-6.8	-6.3

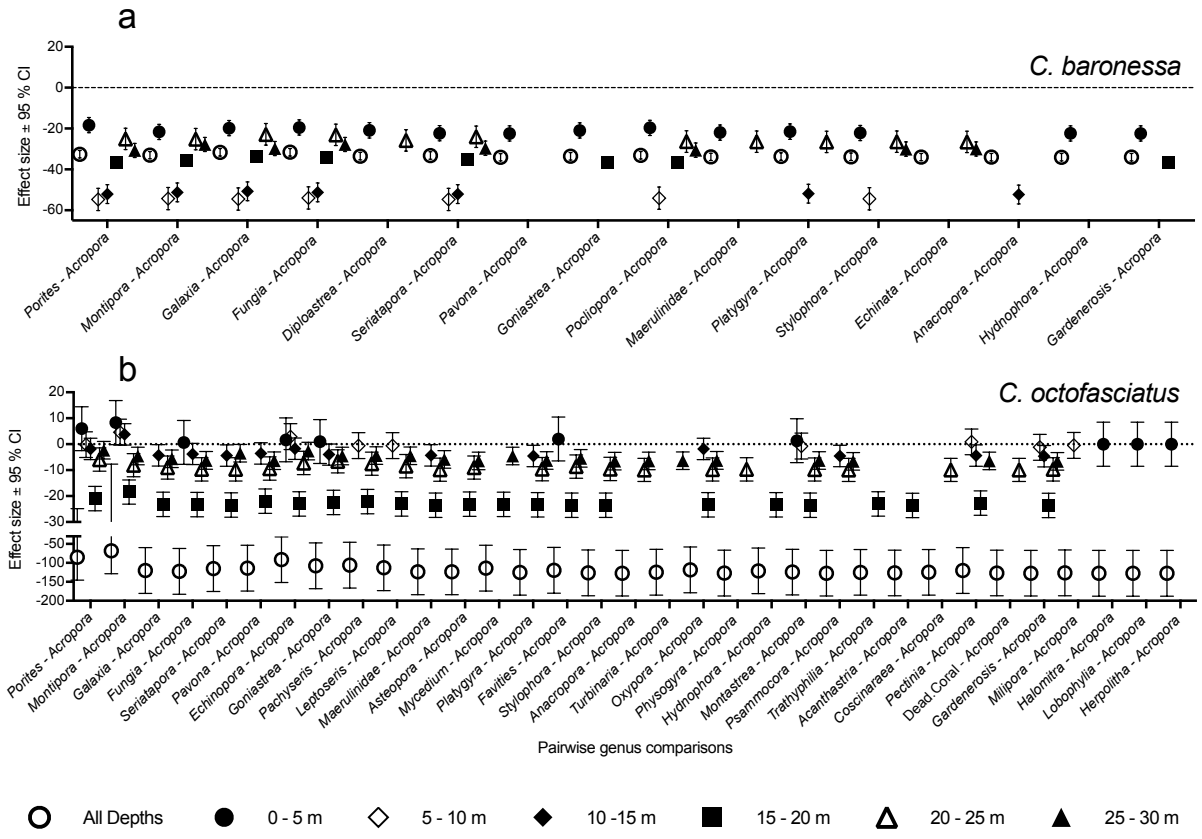

Figure S1: Plots of the effect sizes for pairwise comparisons of the proportion of bites taken from *Acropora* compared to each other targeted coral genus in 5 m depth bins between 0 m and 30 m for two obligate coral feeding butterflyfish species: (a) *Chaetodon baronessa* and (b) *C. octofasciatus*. Comparisons where the 95% confidence intervals do not cross 0, are indicative of significantly different feeding effort on each genus ($\alpha = 0.05$).

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